

## MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. XI.

## EVOLUTION OF CHARACTERS IN THE ORDER: VENATION OF THE NEMESTRINIDAE.

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(Two Text-figures.)

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*Foreword.*—The direction which the evolutionary trends in Diptera is presumed to take, is given by Williston (1908), his main idea being developed below, as on present evidence it remains satisfactory, though published thirty-seven years ago. Since Williston wrote, however, doubt has arisen as to whether the terms applied to the structures of the Diptera are in accord with homologies of other orders, and amendments are being suggested by various morphologists to rectify the position. These amendments are advancing the formation of a phylogenetical classification and, in addition, it is now possible to render into simple sequence some complex and apparently interrelated minor developments that are used in taxonomic work.

Regarding the present study of venation in the Nemestrinidae,\* it must be noted that considerable confusion exists in the interpretation of main veins and cross-veins, no method being known to determine their status other than by comparative morphology. Alexander (1928) has shown that the so-called cross-vein between  $R_1$  and  $R_2$  is the vein  $R_2$  itself coalescing with  $R_1$ . He gives a supernumerary vein between  $R_1$  and  $R_5$  which was originally regarded as being part of  $R_1$  at its furcation with  $R_5$ .

This development suggests that the second radial-median cross-vein in the Cyrtidae may be the vein  $M_1$  coalescing with  $R_5$  and the supposed  $M_5$  coalescing with  $M_1$  is due to a cross-vein, and is not part of a main vein. In the ultimate, it is expected that the veins holding the same position in the wings of various families are not all homologues, but it is customary to retain the Tillyard notation until valid reasons are given to make a change.

I am indebted to Mr. Lucius Allen, B.A., for abbreviating some of the paragraphs of my manuscript, and to Professor E. F. Simmonds for mathematical aid when determining the sequence of shapes evolved in the varied abdominal forms, a summary of which is given below. Also Mr. Edgar Riek, B.Sc., recently rediscovered the wing-folding mimetic fly at Sunnybank (September, 1944) and studied it with me on a comparative basis with its model, thus enabling the account below to be more detailed than otherwise would have been the case.

*The Longitudinally Folding Wings.*—The flies *Cerioides subarmata* C. & B. and *C. alapllicata* Hardy (Syrphidae) have wings that fold longitudinally in the manner

\* The notation of veins given by Tillyard does not conform to homologies of veins within the order. So far Alexander has shown that in the Nemestrinidae there is one link with a branch of the Tipuloidea, so presumably this is a connection leading to the Tabanoidea. In the Cyrtidae there are two radial-median cross-veins which is the number also traced in the Syrphoidea and may prove another link between two superfamilies if the morphological affinity between these two families is correctly assessed by Crampton. Clues like these are rare and hard to identify, and each author placed his own valuation on their significance. In Tillyard's view there can hardly be two radial-median cross-veins, and in manuscript he notated the second in the Cyrtidae as being  $M_1$  which, if correct, suggests that  $M_1$  is eliminated from the veins of most Syrphidae. This and other consequences may make Tillyard's notation for the Muscoidea utterly collapse. There can be no scheme of venation yet acceptable to cover the Diptera, but the Tillyard scheme already is modified for the Tipuloidea along phylogenetical developments, and, in its constituent parts, the radial field is notated differently one from the other, agreeing with the Tillyard notation only in the Tanyderidae.

somewhat resembling the folding wings in *Diptoptera*, thus enhancing the fly's resemblance to those wasps (Hardy, 1933, p. 420). The flexure in both cases is evidently automatic as it occurs only when the wing is brought back to the resting position and, at least on the wasp, no musculature of the forewing can be involved; in other respects there are marked differences in the manner of this flexure.

In the wasp, starting from the apex of the line, the flexure usually crosses the tip of the median vein, but sometimes lies behind it, and reaches the posterior wing border near the base, passing through the area between the median and cubital veins, and crosses the cubital vein where this is slightly flattened and broadened. The folding takes place along this line in a manner that brings the posterior part of the wing to lie below the anterior part, venter to venter.

In the fly the line of flexure runs from the wing margin between the median and radial veins, crosses the media apically where it bends rearwards and without affecting that vein, then follows the strong crease adjacent to the media through the vein  $M_{3+4}$  which is strongly depressed at this point of furcation and perhaps completely broken there; the flexure coincides with this crease to reach a considerable distance along it to a point from where it passes over the fold just anteriorly placed to the vein bordering the alula along which the flexure reaches the wing margin behind the wing base. Those wing sclerites lying at the base, one each side of the median crease, anteriorly and posteriorly, appear to move towards each other when the wing is folded in a manner that brings the posterior part of the wing to lie above, nearly touching, the anterior part, meeting dorsum to dorsum. It is not certain if this apparent motion of the wing sclerites be due to the motion of the folding only, as it might be due in part to some undetected muscular action perhaps causing the flexure.

That break at the furcation of the median vein may yet be detected more widely than is at present known, for it occurs in the genus *Apiocera* (see Norris, 1936, p. 54), and is known as the thyridium on other extant orders and in some fossil wings. This thyridium may have some connection with wing folding wherever it occurs and thus indicate that once wing folding was more widespread. Further evidence may be indicated by wing-folded pupae of the families *Blepharoceridae* and *Simuliidae*, leaving fold-creases in the adult which no longer folds the wings.

Those flies that have an upward flexure of the alula when the wings are brought to rest show that presumably the jugal fold is all that remains in these cases of what may have been a more complete folding system, and other flies are showing indications of wing folding in other ways.

*The Transversely Bending Wings.*—Nearly all other flies known to me, including other *Ceritoides*, retain the wings expanded in the one plane apart from the alula already mentioned. The few exceptions have wings that bend transversely when at rest and do not complete the folding. This transverse flexure is found in the *Psychodidae*, in the genus *Ophiodesma* (*Stratiomyiidae*), in certain flies of the *Acalyptrata* and in the genus *Chlororhina* (*Calliphoridae*), thus showing a wide distribution over the order with the maximum bending in the *Psychodidae* where the wings have a downward flexure with an acute angle near the base, and in the others forming an obtuse angle at or beyond half-wing length. In the *Blepharoceridae* there is a transverse crease marking a line of folding that is comparable to this line of flexure in the *Brachycera* and which may have had the same origin.

*The Vena Spuria.*—Possibly that convex *vena spuria* found in most *Syrphidae* is another survival of a primitive character, marking a remnant of some former condition in so far as creases in other families strongly suggest that these once had a *vena spuria*, too. Lundbeck (1916, p. 33) states that ". . . in *Bombylius* we find a wing-fold much recalling the *vena spuria*", and although there are many similar traces elsewhere, this character is missing in Australian species of *Bombylius*.

The claim that the *vena spuria* is a spurious vein rests upon the fact that it cannot be brought into alignment with any notation of veins, but all notations are unsatisfactory, exhibiting many abnormalities which are not explained.

*The Colours, Hairs and Processes.*—The eye-colour and the body-colour, already discussed in these PROCEEDINGS (Hardy, 1939 and 1940 respectively), may sometimes

depend upon a fundamental alteration like that which brings variegated eye-colouration and the development of a powdery covering which produces a new range of colours on the body, but the nature of these developments is not understood. The change that takes place in the terminal structures (Hardy, 1944) and the development of bristles, tubercles, spines, etc., are features that appear to become increasingly complex and then simplify, finally disappearing, leaving hardly a trace of the phenomenon in the advanced stages.

Spines that arise from the cuticle as local protuberances must not be confused with those granulations that may cover wide areas and are formed by deepening hair-pits. A highly roughened surface exhibited in the latter case seems to be associated with a reduction of hair length, and in addition, the more hirsute types of flies, wherever they occur, lie low in the phylogeny of their respective branches. This does not mean that the most primitive flies were densely hairy, but rather that an early increase in hair density may have been linked with the disappearance of something else.

*Two Types of Spine.*—Thoracic spines are found in various but isolated genera and also in all genera and species of the tribe Chrysopogonini (illustrated by Hardy, 1934, fig. 15). These spines have a consistency in size and shape that suggests a considerable stability not equalled by any scutellar spines formed by cuticular projections. It may be true that excrescences of many kinds arise on insects of senile strain, as reported by James (1936), but the cause of cuticular spines, wherever they occur, seems to be the reduction of surface area covered by the sclerite without a corresponding reduction of the volume of the sclerite, mainly that of the scutellum, whereas the development of the pair of spines referred to on the thorax, seems to be linked with the elimination of vestiture, since each of these two hairs is transformed first into a strong bristle, then into a spine, and the rest of the mesonotum is left bare.

*Antennal Tubercle.*—A trend towards developing an antennal tubercle occurs widely over the order and is well known in the genus *Cerioides* (illustrated by Nicholson, 1927, Text-figs. 1, C and D), where the tubercle is seen to vary from short to excessively long. This development on the fly takes place subsequent to emergence from the puparium and apparently it originated within the subfamily Cerioidinae, not as an inheritance from some more primitive type. By holding the point of a pin against the head at the base of the antennae of a newly emerged fly, it is easy to restrain development of the tubercle, and this action produces no abnormality on the head, nor yet any alteration to the antennae, thus showing that the bulk that would have formed the tubercle has been absorbed within the head mass. Such experiments were carried out on a number of *C. ornata* Saund. reared from waste comb of a beehive; the tubercle also was stunted in its growth by similar experiments at later periods. Occasionally flies with a shortened tubercle are caught, the full extension of the tubercle evidently having been prevented by some extraneous circumstance.

*The Articulating Scutellum.*—It is difficult to interpret the case of the articulating scutellum (described by Hardy, 1944, p. 61) in *Neoxaireta spinigera* Wied. (Stratiomyiidae) one of the so-called mimetic flies with pictured wings and clubbed abdomen, both evidently rather primitive characters. Here the scutellum is spined and is hinged to swing up and down in unison with the motion of the wings, whilst (at least on the relaxed fly) the halteres move in the opposite direction. If this be a true scutellum, then a unique character has arisen without any apparent utility. If, however, it be the true metanotum, as has been claimed, then it becomes obvious that the muscles of articulation survive from those of the metanotum. A claim may yet be made that it is the true first tergite of the abdomen.

*The Upstanding Scutellum.*—This articulation of the scutellum may account for the various angles at which the scutellum is set within the Stratiomyiidae, notably in the tribe Pachygasterini, where some species are found with the upstanding scutellum as opposed to the normal horizontally fixed form.

As opposed to this true type of upstanding scutellum is another found in some Therevidae (illustrated by Mann, 1929, fig. 2, D), which is caused by an enlarged tubercle arising from the dorsal surface of the scutellum which itself is horizontally held as seen by the marginal bristles lying on the true apical margin below the tubercle. This



upward thrust of the dorsal surface could be caused by shrinkage in the length of the scutellum without sufficient reduction in bulk.

*Abdominal Shape.*—The shape of the abdomen is fairly consistent within a genus, few genera showing any marked variation amongst the species. Such variation represents slightly different stages in the evolutionary process and is not sufficient evidence to indicate a complete sequence of changes. It is convenient to assume that the primitive shape was cylindrical with most segments as long as, or a little longer than, they were broad. The advance can then be conceived as taking two trends in conformity with increasing egg-capacity. The abdomen becomes either (*a*) attenuated with each segment over three times longer than broad, or (*b*) broadened so that each segment becomes over three times broader than long, both these proportions being within those observed on flies.

When these two trends appear in different segments of the abdomen of one individual, the two possibilities are realized, viz., the tapering abdomen that widens basally (*c*), and the clubbed abdomen that widens apically (*d*). In the former case, that is in (*c*), there develop the shortened basal segments (*e*), and the highly reduced apical segments (*f*) (the so-called "postabdomen"), whilst from the combined (*e*) and (*f*) there evolves the sphero-conical abdomen (*g*), the form seen in most Muscoidea.

Reduced to the simple components (*a*) and (*b*), it is conceivable that many shapes can be brought about by adjusting length, breadth and depth of the abdomen without altering the total surface area and capacity of the abdomen, but if one alone were used, then (*a*) would result in a reduction in volume or capacity of the abdomen relative to surface area, and (*b*), becoming spheroid under practical conditions, would increase the relative capacity as can be seen mathematically through the well-known theorem in the calculus of variations which states that for any given surface area, the volume is greatest when the surface is a sphere. There is a marked trend to produce the sphero-conical abdomen throughout the order, and the character even occurs in flies carrying what may be regarded as primitive characters.

Amongst the long series of shapes derived from the cylindrical form is that in which the abdomen is broadened in the middle segments. In this type, because of the necessity to maintain a reasonable capacity, the abdomen becomes depressed and assumes the depressed oval form, and through further shortening finally reaches the disc shape as found in many Stratiomyiidae. Further, it is easy to trace the development from the cylindrical to the conical and to the sphero-conical shapes, and also the trend towards the clubbed form which is evidently quite an early evolved type as it is based upon a rather primitive cylindrical abdomen.

*Mimetic Pattern.*—It is thus seen that abdominal formation, like mimetic colours discussed by Hardy (1940), is an inevitable process that needs no "enhancement by natural selection", as Nicholson (1927) and others have supposed, "in order to satisfy the phenomenon of mimicry". If there be any natural selective agency playing its part in the matter of mimetic Diptera, it would be in maintaining these mimetic characters which form part of the normal process of development, coming low in the series of developing characters, and in preventing them from proceeding to more advanced characters. Environmental factors are maintaining, but did not produce the mimicry.

*The Old Theory of Development Revised.*—Throughout my investigations on characters of Diptera, I can find no sign other than that leading to the conclusion that most characters have a potential distribution over the whole order, the same structures being induced and eliminated widely, whilst colours are being developed in succession, each colour in its sequence, following one after the other. James (1936) credibly states that "In general, there is reason to believe that reduction in parts is a sign of evolutionary development . . .", whilst Williston (1908) forestalled the view in his discussion, giving nine cases of such reduction, a process which he believed to be irreversible, all or nearly all being polyphyletic, resulting in numerous cases of parallel resemblances. Finally he suggested that the *Nycteribia* and *Mallophaga* are perhaps the most highly specialized of all insects, having travelled furthest from the starting point. Some of Williston's remarks are not justified in the light of recent information; nevertheless, the general trend of the idea remains undisputed. Each of those characters he quotes must

have developed at the time of building up and isolation of the order and now has reached its period of elimination, leading one to suppose that reduction in parts is the only criterion of progress.

*The Theory of Compensatory Adaptation.*—Some characters and combinations of characters would seem to have a lethal effect as they develop a stage that does not permit adaptation to changing environment, and that ultimately must eliminate the line carrying them. Apart from these, the development of new characters may serve the purpose of compensation for characters that are lost in the mutual loss and gain taking place between them. Practically every new structure developed is accompanied by a diminution of some nearby structure, or expressed simply, a part increases with the diminution of some other part and *vice versa*. It becomes increasingly apparent that following on the loss in adjacent parts, the structures which compensate for the loss may, in a similar manner, dwindle and disappear at some subsequent stage, the new loss being usually compensated by further developments. In all cases, however, the total loss exceeds the gain, making a net loss phylogenetically and reaching simplicity of structure in the ultimate result.

The whole conception may be rendered clearer if it be assumed that the distinguishing characters between species are reflecting only the different stages reached by each character in the inevitable sequence through which the varied characters are passing. During the progress of time some of these characters are retained indefinitely whilst others pass away again relatively soon. The summation of characters forming the individual species may appear to be a complex, each character diverging "fan-shape" in the various species from the parent stock, but this is due to the various tracks taken by them under the influence of the evolutionary process, and actually the drift is towards a final simplicity to which all tracks lead. Just as there is a line of progress to be traced arising from the common ancestral form that existed in the remote past, so also there is a general simplification towards which the ultimately surviving types may drift, no matter how complex the intervening tracks taken appear to be.

*The Application of the Theory of Compensation to Taxonomy.*—The manner in which taxonomists are arranging the order Diptera is promoting this idea of compensatory characters, but in many cases the authors reverse the sequence of development, regarding, as they do, a simple unspecialized character as primitive, and those forming side issues and destined to disappear relatively soon, as being advanced or highly specialized characters, there being no data upon which to check such conclusions. Many of their views are demonstrably wrong on evidence already accumulating. In the ultimate, numerous characters are both advanced and primitive, so that, unless qualified, the use of these terms may mislead. If used as a working hypothesis, the present theory may lead to better interpretations of characters and more definite conclusions in phylogenetical studies.

*The Application to Studies in Terminalia.*—The trend already seen in the development of terminalia, is to transform parts into structures hard to recognize in the new form, whilst new processes and depressions may arise and become incorporated with the transformations. Fantastic shapes may develop, these being devoid of any apparent utility, but some may become adapted to useful purposes though not essential ones. The main features affecting development in the Muscoidea have been dealt with independently by Crampton (1936) and by Hardy (1942), this superfamily clearly showing the complicated nature of the subject; but the two authors are not in agreement about details. Hardy (1934) has shown the development for the Asilidae, this being wholly by reduction in the female.

*The Transposition of Claspers.*—There is nothing in literature that may suggest how it comes about that in the Tabanoidea the claspers are hinged to swing laterally and in the Asiloidea vertically. Quite obviously the Tabanoidea retain the primitive form and the Asiloidea have developed a secondary pair of claspers, having lost the primary pair everywhere except, perhaps, in the Bombyliidae. A possible intermediate stage is found in the Nemestrinidae where, as in the Bombyliidae, the claspers have moved upwards to lie on the dorsal surface. Whereas in the Nemestrinidae the claspers swing laterally in the normal way, those in the Bombyliidae swing vertically as seen in other Asiloidea.



This may have been brought about in the Bombyliidae, by the supports of the claspers moving ventrally to form one fused unit on the ventral side of the terminalia, no longer being laterally placed, and thus displacing the direction of muscular tension. In the Nemestrinidae, the presence of claspers on the dorsal surface of the supports which remain laterally placed, does not alter the muscular tension and they move laterally as elsewhere in the Tabanoidea. Besides the claspers, however, there occur what Mackerras regards with some doubt on its homologies, as being the basi-dististyles. The pair of basi-dististyles curve upwards and arise from a low position on the clasper supports, taking the form very much like most claspers in the Asiloidea and may possibly be homologous with them. These basi-dististyles have a very limited arc in which to swing laterally, and the apices, being near the claspers, restrict the arc of swing of the claspers. There is nothing of this movement suggested by Mackerras but it was observed on a specimen of *Trichophthalma bivittata* Westw. (E. Riek, Sunnybank, August, 1944) given to me for study whilst in the relaxed condition.

There has been a recent tendency by authors to bring the Nemestrinidae and the Bombyliidae together on the basis of their adult structure, but differences in larval structure, the female terminalia and other characters separate them into different superfamilies. The supposed affinity evidently denotes a common ancestry, but mainly with parallel development playing the leading part.

*General Remarks.*—James (1936), dealing with some evolutionary trends in the Stratiomyiidae, gives an essential outlook that varies slightly from the present one, expressing the view that scutellar spines come and go, but he does not carry his observations to the extent here outlined, and further, there are some modern taxonomic papers showing agreement in the manner in which the authors adopt phylogenetical lines of classification and show a very evident progress by reduction of parts, and comparatively few new structures are evolved in any one branch. The most striking differences in structure are arising through modifications in size and shape of existing parts, and some of those that might appear to have arisen *de novo* are certainly primitive and largely obsolete. Amongst these rare survivals are three classed as such above, namely, the folding wings of a mimetic fly, the *vena spuria* of the Syrphidae and the articulating scutellum of a Stratiomyiid fly. Hitherto a large part of the broader lines of classification in the Brachycera has rested upon wing venation, about which very little is adequately understood (as indicated below) and the homologizing of the veins within the order is not yet complete. Tillyard considered no difficulty was in the way of constructing an archetype for the order, but when this was done it was found that the data gathered, subsequently failed to fall into alignment. It may be better to form an archetype for each family on an independent basis and work back to that of the order through the archetype of superfamilies.

#### VENATION OF THE NEMESTRINIDAE.

*The Radial Field.*—Alexander (1929) has shown that in some extant Nematocera the radial sector is dichotomously twice branched, which is in agreement with the generally held theory of the Dipterous venation and is made to cover the whole order irrespective of exceptions that were becoming apparent. The radial field in some Nematocera has five distinct branches, but in the ascending scale these become reduced to four, which is the maximum number found in Brachycera. The first branch of the radial sector,  $R_2$  is definitely shown to coalesce with  $R_1$  and traces of this are left in the apparent cross-vein joining  $R_1$  and  $R_3$ , erroneously called the interradial cross-vein by Tillyard. This condition is traced in the Brachycera by  $R_2$  coalescing with  $R_1$  in the genus *Nycterimyia*, and there is no reason apparent to dispute the idea that it was in this manner that the radial field in the Brachycera became reduced to four veins.

Another feature of importance found by Alexander in the Tipuloidea is the transferring of the dichotomously twice-branched radial sector to the pectinate type. On this account the radial sector first furcation divides  $R_5$  from the main stem and  $R_4$  divides away separately; finally  $R_8$  leaves  $R_2$  coalescing with  $R_1$  towards its apex, the evidence of which is seen in *Nycterimyia*.

The vein  $R_1$  branching away independently from the main stem and its partial disruption, forming the "appendix", is sufficiently wide in distribution amongst the Tabanoidea and Asiloidea to indicate that this happens in the Brachycera. In this interpretation of the radial field Alexander assumes that a supernumerary vein occurs between  $R_4$  and  $R_5$  and it is best to regard this as a cross-vein that became important, permitting the elimination of the basal section of  $R_4$ , and finally gave the deceptive appearance of  $R_4$  branching from  $R_5$  that misled earlier authors.

This outlook leads to a better interpretation of the radial field in the family Nemestrinidae and apparent anomalies are thereby explained.

*The Median Field.*—According to Mackerras (1925), the genus *Exeretoneura* resembles the Leptidae very closely, the wing being primitive in shape as also is the disposition of  $M_4$ . If this be so, then on Tillyard's basis of notation a reasonable interpretation of the median field would be along lines adopted by him for the Leptidae and Tabanidae, but the manner in which Mackerras treats the venation not only shows divergence from the Leptid type but also shows a cross-vein between  $M_3$  and  $M_4$ . A cross-vein in this position is unusual but occurs in the Tanyderidae, and its presence has yet to be shown in any family of the Brachycera. Usually the vein  $M_3$  takes the position of this cross-vein by coalescing with  $M_4$  but it is not certain that this always occurs, certain primitive genera being possible exceptions. It is usual to regard this possible cross-vein, wherever it occurs, as being the course of the vein  $M_3$ , a policy followed here. The supposedly similar cross-vein in *Nycterimorpha* is certainly a main vein, and when so treated it clarifies a very confusing type of venation.

Between the bend of vein  $M_3$  and the oblique vein in *Exeretoneura*, occurs the intermedian cross-vein ( $i-m$ ) permitting the coalescing of  $M_3$  and  $M_4$  to reach the wing margin at a point remote from the oblique vein. When  $i-m$  becomes eliminated, it brings  $M_{3+4}$  to lie near the apex of the oblique vein, whilst  $M_2$ , originally at the apex, takes a position parallel with  $M_1$  as seen in *Trichophthalma* and other genera.

*A Summary of Wing Characters.*—The figures (Figs. 1 and 2) represent all the characters discussed in the radial and median fields of Australian genera, the broken lines representing the course of veins that have disappeared. In no case has  $R_4$  shown a trend to coalesce with either  $R_3$  or  $R_5$  which is seen to occur in exotic genera.  $M_1$  may coalesce apically with either  $M_2$  or  $R_5$  in both Australian and exotic genera. Very few supernumerary veins ever occur between the branches of the radial sector and the median field reaching the hind border of the wing, but are common in some exotic forms including *Nemestrina aegyptica* Wied., which has quite a network over the area. A supernumerary vein is not known to occur between  $R_1$  and  $R_5$ .\*

Figure 1 represents a hypothetical type of venation showing the manner of notation of the veins and may even represent the archetype. It is possible, however, that another cross-vein will be needed to represent the true  $M_1$  which would then leave that part of  $M_3$  adjacent to  $M_4$  to be regarded as a cross-vein, which it was considered to be by Mackerras although he did not state his evidence. An appended figure shows the position of this possibly true  $M_1$ .

\* According to Alexander (these PROCEEDINGS, lii, 1927, 48), in some Tipulidae a supernumerary vein occurs between  $R_1$  and  $R_5$ , whilst a cross-vein that is similarly placed always takes the oblique form or is in series with the vein branches and is never transversely placed in the manner of that supernumerary vein. Theoretically the supernumerary veins are the remnant of the "lace-wing" type of venation of the pre-Dipterous ancestry, and the cross-veins are the persisting supernumerary veins placed advantageously for maintaining mechanical strength during the course of vein reduction. Main veins are simple or branched units, but some so-called branches may be complexes, with a cross-vein formed in series with two remnants of branches, appearing as a single unit. Any two or more branches join to form a complex, the maximum development being on *Neorhaphiomidas* (Apioceratidae) where two of the median branches conjoin all the radial branches in a common apex. Further complications arise with partial and total elimination of branches.

As far as I know supernumerary veins are liable to occur only in some Tipulidae, most Nemestrinidae and occasionally in the Bombyliidae and even in the Asilidae and are interpreted in accord with the notation adopted just as are the cross-veins.

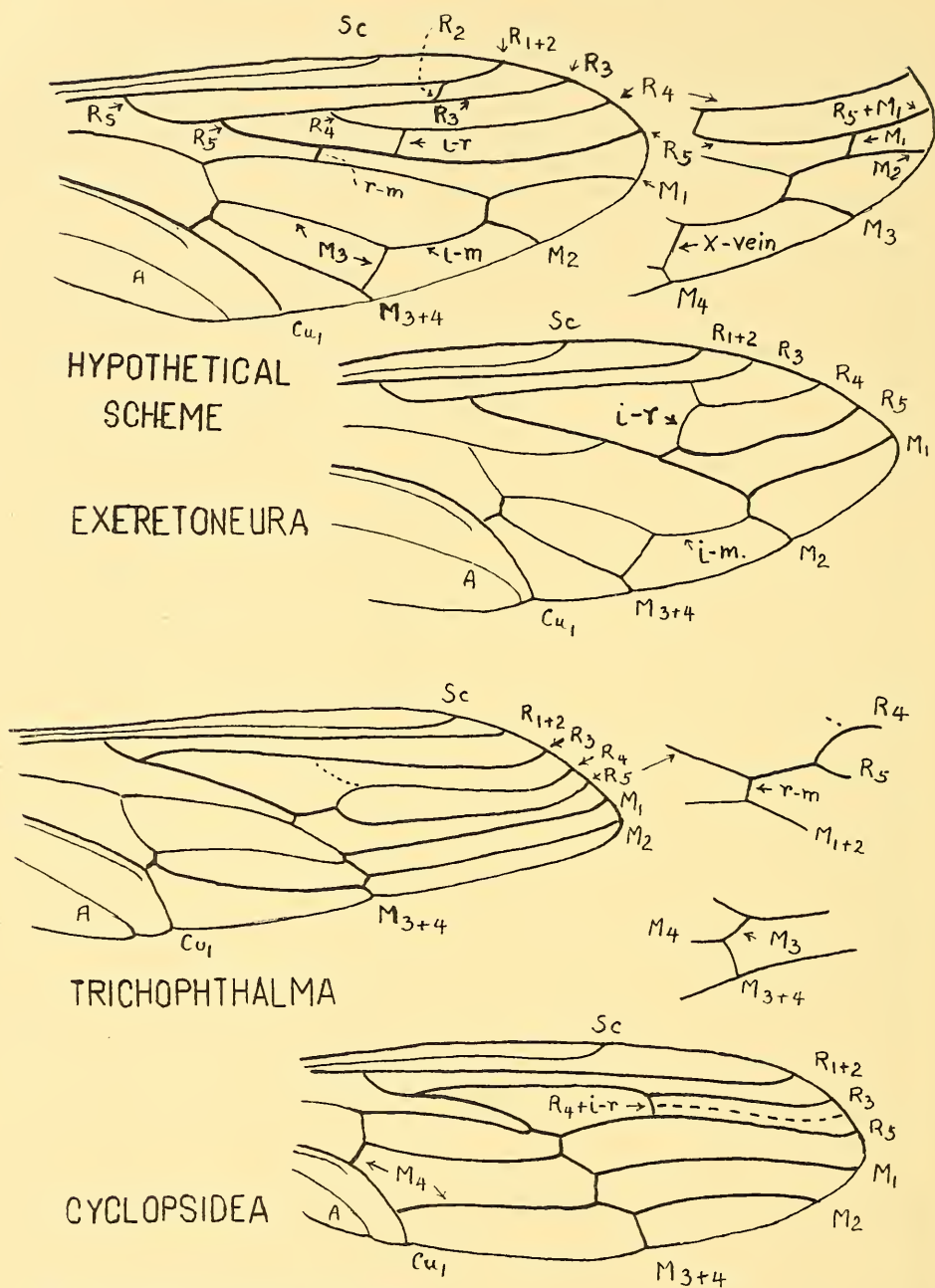


Fig. 1.—Venation of the Nemestrinidae.

Sc, subcosta; R, radial field, the branches being marked by numerals;  $R_5$ , radial sector at its furcation with  $R_4$ ; M, median field with branches marked by numerals;  $Cu_1$ , cubital vein; A, anal vein; *i-r*, interradial cross-vein; *r-m*, radial-medial cross-vein; *m-cu*, median-cubital cross-vein.

The oblique vein crossing the wing at an angle is composed of parts of various veins in the radial and median fields and is also called the "diagonal vein". This oblique vein is not formed in the hypothetical scheme which venation is itself very like that in the Cyrtidae. The figure shows the position of a second radial-medial cross-vein in the Cyrtidae and which may be the true vein  $M_1$ , and if so the cross-vein then becomes apparent between  $M_3$  and  $M_4$  as discussed in the text. Separate sketches show some details in the venation of *Trichophthalma* and broken lines represent the course of veins that are missing in the various genera.



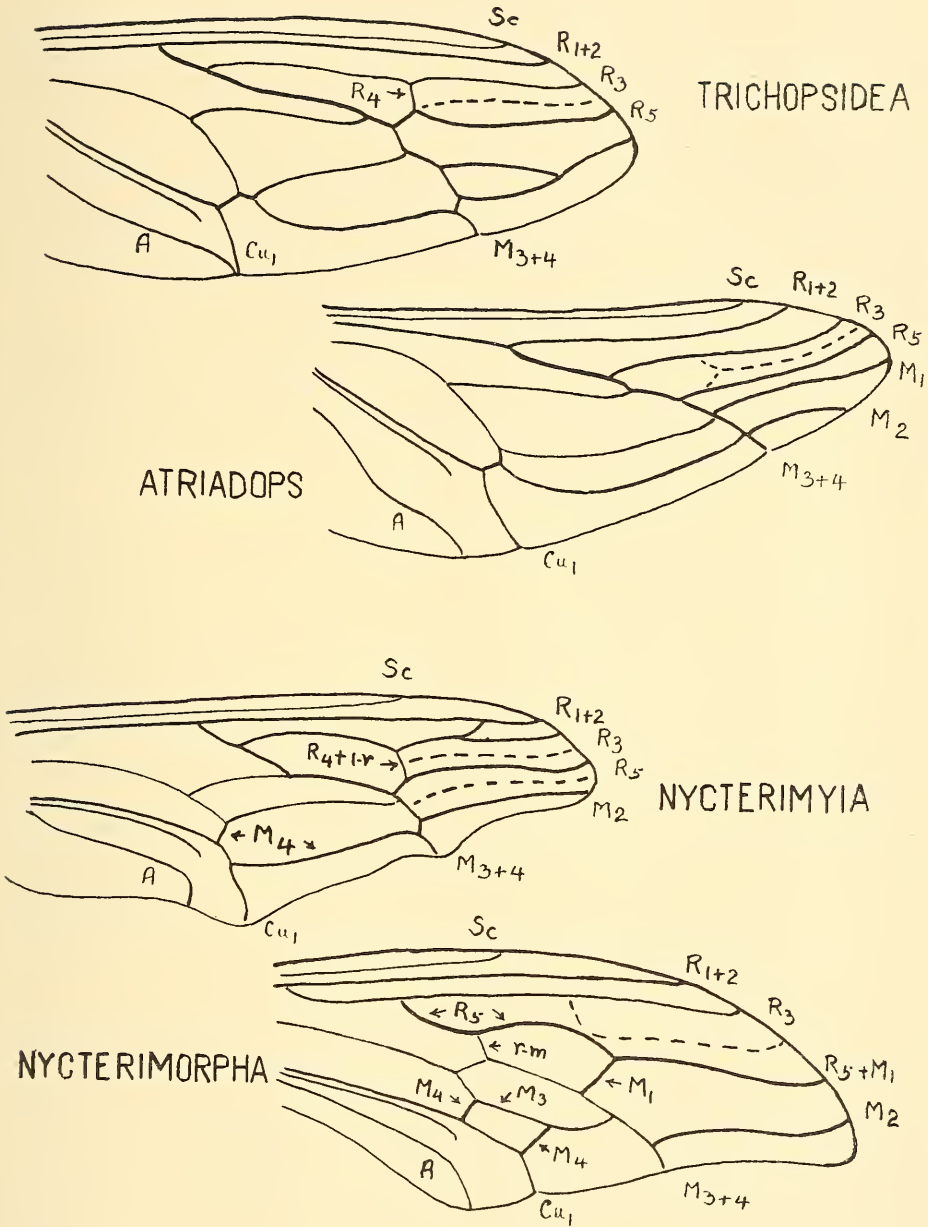


Fig. 2.—Venation of the Nemestrinidae. (For explanation see below Fig. 1.)

The accompanying table of characters gives a summary of twelve points that are apparently important for phylogenetical consideration and are divided into those of primary or primitive nature and those of advanced development. These two grades are complementary but distinct identities.

Seven primary characters are listed and it will be noted that *Exeretoneura* and *Nycterimorpha* do not have any in common. Between these two genera come *Nycterimyia* and *Trichopsidea* with one, *Atriadops* and *Cyclopsidea* with two, and *Trichophthalma* with three out of the five carried by *Exeretoneura* which, together with *Trichophthalma*, bears none of the advanced characters recorded.

In *Trichopsidea* the vein  $M_1$  coalesces with  $M_2$  and there is a trend for  $M_3$  and  $M_4$  to coalesce at their bases (i.e., become stalked). In *Atriadops* these two veins remain apart, and the basal coalescing of  $M_1$  is with  $Cu_1$  in *Nycterimyia* and *Cyclopsidea*, a condition that leads to the abnormal development in *Nycterimorpha*. In this last genus the apical coalescing of  $M_3$  and  $M_4$  is far in advance of the oblique vein, and gives the venation a peculiar character, which Mackerras had difficulty in elucidating.

The various veins are depicted in the figures on the present interpretation and the distinguishing features there seen are incorporated in the following key which has a phylogenetical basis. *Nycterimyia*, *Atriadops* and the abnormal *Nycterimorpha* are so closely akin that the venational differences may prove to be only subgeneric in value. The related *Trichopsidea* is parasitic on grasshoppers and it seems probable that the other three are also parasitic on Acridioidea.

*Key to Genera of Australian Nemestrinidae.*

1. With four radial veins reaching the margin independently ..... 2  
     With only three radial veins reaching the margin, the vein  $R_4$  being eliminated or nearly so ..... 3
2. With the furcation of  $R_4$  from the radial sector present and only one median vein lies parallel with  $R_5$ . The veins  $M_3$  and  $M_4$  remain remote from the oblique vein ..... *Exeretoneura* Macq.  
     With the furcation of  $R_4$  from the radial sector obliterated. Two median veins lie parallel with  $R_5$  and the veins  $M_3$  and  $M_4$  are approximate to the apex of the oblique vein .... *Trichophthalma* Westw.
3. With  $R_4$  at its furcation from the radial sector, together with the cross-vein  $i-r$  forming a secondary cross-vein between  $R_3$  and  $R_5$  ..... 4  
     Without such secondary cross-vein,  $R_4$  and  $i-r$  being entirely obliterated ..... 5
4. With  $M_1$  and  $M_2$  reaching the wing margin independently ..... *Cyclopsidea* Mackerras  
     With  $M_1$  and  $M_2$  coalescing before reaching the wing margin ..... *Trichopsidea* Westw.  
     Only one free median vein present,  $M_1$  being absent.  $R_2$  is present at its furcation from the radial sector (unique) ..... *Nycterimyia* Lichtw.
5. With veins  $M_1$  and  $M_2$  lying parallel with  $R_5$  and reaching the wing margin independently ..... *Atriadops* Wandol.  
     With veins  $M_1$  and  $R_5$  coalescing apically for a considerable distance, leaving only  $M_2$  lying parallel with  $R_5$  ..... *Nycterimorpha* Lichtw.

TRICHOPTHALMA BIVITTATA Westw.

Westwood, *Philos. Mag.*, Lond., vi, 1835, 448; Edwards, *Dipt. Patagonia and S. Chile*, v, 1930, 180. *T. eques* Schiner, *Reise Novara Dipt.*, 1868, 110.

This species is the genotype of *Trichophthalma*, the identity of which species has been confirmed by Edwards, who examined the type, recording the matter in a footnote. Schiner's name, under which the species has long been standing in collections, becomes a synonym. Care is needed to avoid confusion between the names *bivitta* Walker and *bivittata* Westwood, both species being plentiful in collections and belonging to different series. Confusion made by earlier authors in this respect has been clarified by Hardy (1924) and by Mackerras (1925).

*Hab.*—New South Wales and south-eastern Queensland.

CYCLOPSIDEA HARDYI Mackerras.

Only one specimen is known and was captured by Mr. J. H. Buzacott of the Queensland Sugar Bureau, and not by myself as recorded erroneously by Mackerras.

Owing to an accident before returning to me, only the terminalia are now left, so the published figure of the venation has been used to interpret the characters.

A Comparative Table of Characters.

Genus.	Primary Characters.							Advanced Characters.					Total.		
	4 radial veins.	R <sub>2</sub> present at furcation.	r-m present at least occasionally.	i-r present.	i-m present, making M <sub>2-4</sub> remote from oblique vein.	M <sub>1</sub> and M <sub>2</sub> free at apex.	M <sub>1</sub> free at base.	M <sub>1</sub> and R <sub>5</sub> coalesce.	M <sub>1</sub> and M <sub>2</sub> coalesce.	M <sub>1</sub> absent.	M <sub>1</sub> and Cu <sub>1</sub> coalesce at base.	M <sub>2</sub> and M <sub>1</sub> coalesce apically in advance of the oblique vein.	Number of primary characters retained.	Number of advanced characters developed.	Number of primary characters in common with <i>Ezeretoneura</i> .
<i>Ezeretoneura</i> ..	+	-	-	+	+	+	+	-	-	-	-	-	5	-	5
<i>Trichophthalma</i>	+	-	+	-	-	+	+	-	-	-	-	-	4	-	3
<i>Cyclopsidea</i> ..	-	-	-	+	-	+	-	-	-	-	+	-	2	1	2
<i>Trichopsidea</i>	-	-	-	+	-	-	-	-	+	-	-	-	1	1	1
<i>Atriadops</i> ..	-	-	-	-	-	+	+	-	-	-	-	-	2	-	2
<i>Nycterimyia</i> ..	-	+	-	+	-	-	-	-	-	+	+	-	2	2	1
<i>Nycterimorpha</i>	-	-	+	-	-	-	-	+	-	-	+	+	1	3	-

#### TRICHOPSIDEA OESTRACEA Westw.

The following note is taken from the typescript minutes of a meeting of the Entomological Society of Queensland, held on the 11th July, 1945: "Mr. Sloan submitted some specimens of Nemestrinid flies and their hosts with the following explanatory note: The bitter bark, *Alstonia constricta*, is a small tree which tends to be a pest in some scrub areas where seedling growth is rapid in established pastures. In some seasons considerable numbers of these trees die and two Cerambycids, *Disterna plumifera* Pasc. and *Prosoplus woodlarkiana* Montr., are sometimes held responsible for the phenomenon. At Bracewell, in March last, dead trees were common but no live insects were present in the wood. However, the twigs were studded with the exit holes normally associated with longicorns of this kind.

On several trees, innumerable flies, each with its wings outstretched, were resting on the twiggy growth. More than fifty could be counted without any difficulty on a single tree eight or nine feet high. The flies were more or less torpid and could be captured . . . by simply enclosing them in a glass tube. Each fly had its ovipositor inserted into one of the longicorn emergence holes and, on sectioning the twigs, innumerable eggs were found inside each cavity. Each hole must have contained 500 or more eggs of the insect."

A few of these female flies submitted to me for identification conformed to *T. oestracea* Westw., though slightly darker, being perhaps denuded of the slight greyish pulverulent overlay on the abdomen. It is evident that they share with some Asilidae the habit of ovipositing into beetle holes though the species has been reared only from grasshoppers. The specific determination needs confirmation on the males.

#### NYCTERIMYIA HORNI Lichtwardt.

Apart from the holotype, specimens have not been recorded in literature, and the species is known to me through a single male specimen in the Department of Agriculture, Brisbane, captured by Mr. W. B. Barnard, at Toowoomba, on the 10th February, 1927. The specimen has its terminalia exerted and held conspicuously in the diverted position.



## ADDENDA.

Mr. E. Riek has informed me that the type of *Cerioides mastersi* Ferg. shows the characters associated with wing folding and the type of *C. apicalis* Ferg. has a very definite thyridium.

A short note "On flies that fold their wings" in *The Entomologist's Monthly Magazine*, lxxxi: 1945, 93-4, draws attention to the implications of this and other anomalies. The abnormal course of veins in Nemestrinidae may be due to the survival of primitive characters. It may be added that in the light of Alexander's discoveries, the breach between the Nematocera and Brachycera appears to be wider than credited, and the Brachycera are not the lineal descendants of Nematocera but instead share with it a common ancestry. Even the venation of Tanyderidae may be inadequate to assess the homologies with the Brachycera.

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